THE MORPHOLOGY OF *BOTRYOPTERIS ANTIQUA*

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THE MORPHOLOGY OF *BOTRYOPTERIS ANTIQUA* KIDSTON

By HENRY SMITH HOLDEN

SYNOPSIS

An account is given of the morphology of *Botryopteris antiqua*, a small fern from the Lower Carboniferous. It discusses the work of previous investigators and re-interprets this in the light of the discovery of additional material. The species is diagnosed and a lectotype chosen.

INTRODUCTION

In 1908 the late Robert Kidston published a relatively short description of a minute fossil fern from the Lower Carboniferous of Burntisland, Fifeshire, which he named *Botryopteris antiqua*. Although his account of the morphology of this plant was, in some respects, incomplete it provided adequate data for its ready recognition by subsequent investigators. Petioles from the Culm of Autun, France, closely resembling those described by Kidston had been known for some time and specimens from this locality were investigated by Pelourde (1910) who, in his paper, states that Kidston regarded the French specimens as being conspecific with those described by him. This view has been generally accepted (Bertrand, 1912 ; Scott, 1920 ; Corsin, 1937) although we have no adequate knowledge of the stems to which the Autun petioles belonged. It is a point of interest in this connection that, whilst with very rare exceptions, the petioles from Burntisland are oval in transverse section those from Autun that have been studied by the author consistently show a well-marked adaxial concavity (Pl. 60, fig. 4) a characteristic also recorded in the specimens from Autun examined by Corsin (1937 : 223, 225). This difference is one of the criteria used in the specific separation of the Cheilanthoid ferns and it suggests the possibility that the French specimens may well belong to a different, though closely allied, species.

Among the more important characters established by Kidston was the fact that the xylem of the stem stele consisted entirely of tracheids without any admixture of parenchyma. He was unable, however, to distinguish in the stem any groups of protoxylem. He also described the main features of the petiole and leaf trace. In the latter he interpreted as protoxylem a band of small tracheids with scalariform thickening normally occupying the more pointed adaxial side of the trace but in some examples, such as that in his fig. 8, forming a narrow band down both sides of the metaxylem and even extending to the abaxial margin. The thickenings of the tracheids of the petiolar metaxylem he described as porose. He also figured a specimen (figs. 11, 12) which he interpreted as being an example of petiolar dichotomy.

Three years after the publication of Kidston's paper Margaret Benson, who had obtained further specimens from Burntisland, gave a fuller description of the plant and, among other things, suggested a different interpretation of some of the sections figured by Kidston (Benson, 1911). Benson's material enabled her to trace the connection between the vascular supply of the petiole and that of the stem and to show that the protoxylem in the petiole was initially mesarch in position. She regarded the plant as " heterophyllous " and considered that the stem bore petioles of two kinds. One of these, which she termed the monarch type, had a single adaxial protoxylem group and was accompanied by a uninerved sheathing organ which she interpreted " as of the nature of an aphlebia ". The second type of lateral structure arising from the stem, which she regarded as a diarch petiole, possessed two adaxial protoxylem groups and was not accompanied by an aphlebia-like structure. She stated that the protoxylem in both types of petiole became " aggregated into one or two adaxial grooves " and that the diarch traces appeared to be preceded and followed by monarch ones. The smaller elements and protoxylem according to her show all intermediate types of thickening from porose to reticulate.

The sections studied by both Kidston and Benson were prepared by grinding down thin slices of the rock containing the fossil until they were transparent enough to be examined by transmitted light. The drawback to sections prepared in this way, especially in dealing with incomplete and frequently fragmentary specimens, is that it is often impossible to be certain of the exact relationships between the separate parts such as stem and petiole and even to be certain that they belong to the same plant. With the advent of modern " peel " techniques some of these difficulties have disappeared and the most recent investigation of *Botryopteris antiqua* by Surange (1952) using such techniques has added materially to our knowledge of the plant. He has established the fact that the tip of the young petiole was circinately coiled (Pl. 59, fig. 3) and has suggested a new interpretation of the morphology differing radically from that put forward by Benson.

Surange interprets the structures termed diarch petioles by Benson as dorsiventral stems from which radial stems, possessing an abundant system of adventitious roots, arise and on which true petioles (i.e. Benson's monarch petioles) are developed in spiral succession. The development of a radially organized stem from the diarch axis is initiated by the separation from it of a lateral trace. This is smaller than the parent axis and carries with it one of the two protoxylem groups. The radial stem, which is characterized by the smaller calibre of its tracheids, develops on the adaxial side of the branch near its base and is adnate to it. Surange states that, in the material examined by him, the structure he terms a dorsiventral stem " invariably gives rise to a radial stem and to no other structure ". He also states that the tracheids of the petiolar protoxylem show spiral thickenings.

Prior to the publication of Surange's paper a number of specimens of *Botryopteris antiqua* from Burntisland had been collected with the intention of making a fuller study of its morphology but, in view of the differing interpretations resulting from the work of the previous investigators to which reference has already been made, it was considered desirable to examine also the sections upon which they had based their views. For this purpose Professor Walton, Head of the Botany Department of Glasgow University, kindly loaned to the Museum not only the slides figured by Kidston but also the whole of the slides of *Botryopteris antiqua* in the Kidston Collection. In addition to these he also loaned slides containing sections of the petiole of *B. antiqua* from the departmental Figured Slide Collection which he had collected from a locality in Dunbartonshire. Professor Jane, of the Royal Holloway College, was equally helpful with regard to the slides of *Botryopteris antiqua* from the Benson Collection as was Dr. Hamshaw Thomas with regard to those studied by Surange. The grateful thanks of the author are due to all these fellow botanists for their ready co-operation. In addition to the Kidston, Benson and Surange slides several from the Gordon Collection were kindly looked out and sent over to the Museum by Dr. O. Bradley of the Department of Geology, King's College, London, and Mr. A. G. Long sent me his sections of the specimen of *B. antiqua* to which reference is made in Surange's paper.

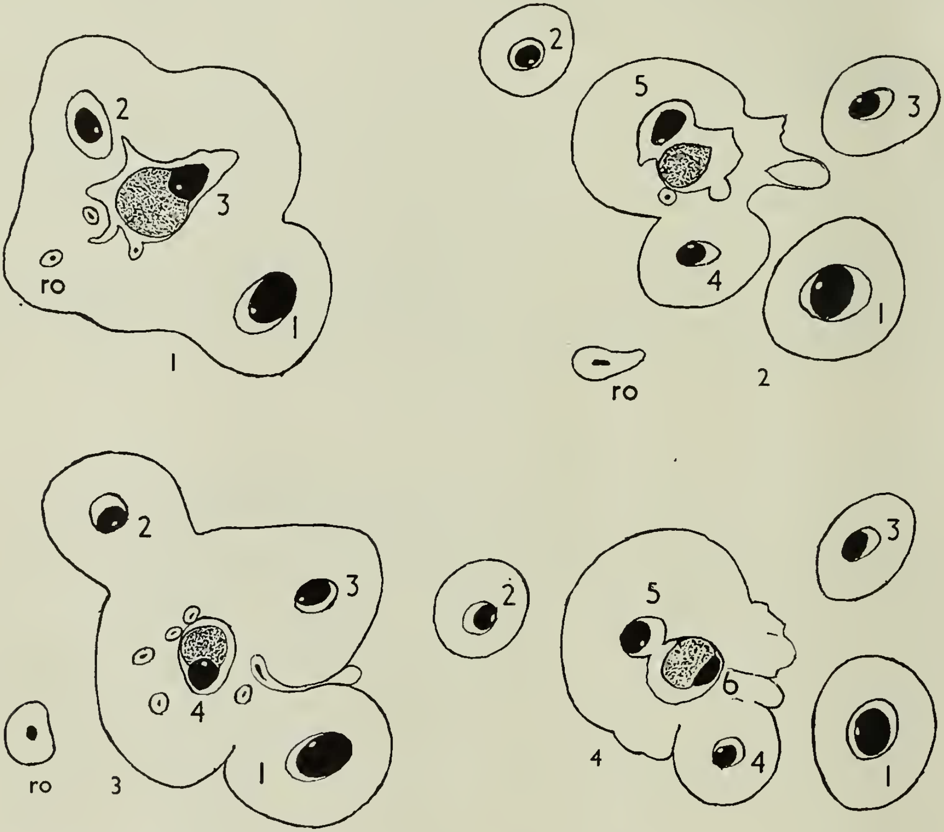
These slides together with those in the Oliver and Scott Collections and that of the author form the basis of the present account but, in addition, a large number of " peels " have been made from blocks of Lower Carboniferous material from that part of the Hemingway Collection which is now in the British Museum (Natural History), Department of Palaeontology. The majority of these " peels " have been prepared by C. H. Shute, Scientific Assistant in the Department.

The study of the considerable number of specimens indicated above, whilst it has not provided an answer to all the morphological problems raised by this Lower Carboniferous fern, has enabled a fuller and more detailed account of its morphology to be given than had been possible previously.

DESCRIPTION

The Stem

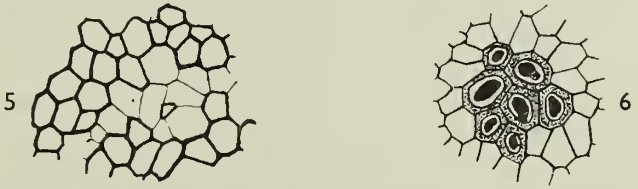
A typical plant of *Botryopteris antiqua* possesses a radially organized stem developing abundant adventitious roots. These roots are most numerous at and near the base of the stem but are also produced quite close to the apex (e.g. Pl. 56, figs. 1, 3). The stem bears closely set spirally arranged petioles which, in many specimens, show a two-fifths divergence (Pl. 56, fig. 1 ; Text-figs. 1–4) though this is by no means constant. Its centre is occupied by a stele which has the shape of a shallow dome. The stelar xylem is composed entirely of tracheids which are smaller in diameter than those of the petioles (Pl. 56, fig. 1) and which show predominantly scalariform pitting though this type of pitting may be replaced by a reticulate type with transversely elongated pits at and near the periphery. Near the stem apex where the differentiation of the tracheids is not completed thin-walled cells occur scattered among the xylem elements which are already lignified (Pl. 59, fig. 6 ; Text-fig. 5). The protoxylem occupies a mesarch position and consists of single minute tracheids or groups of these distributed near the outer part of the stele. The determination of the nature of the protoxylem thickenings proved to be a matter of some difficulty but its spiral character is clearly shown in one of Surange's slides (B 78) and is illustrated in Pl. 58, figs. 1, 2. Neither the phloem and its associated parenchyma nor the inner cortex are preserved in most specimens so that there is a gap between the stelar xylem and the tissues forming the middle and outer cortex (Pl. 56, fig. 1 ; Text-figs. 1–4). There are a few sections, however, in which some or all of these tissues are present and two of these from the Gordon Collection are illustrated in Pl. 56, fig. 2 and Pl. 57, fig. 1. In these sections there are indications that the phloem consisted of a more or less continuous ring of large sieve tubes and phloem parenchyma similar to that occurring in *Ankyropteris corrugata* and many other Palaeozoic ferns. The bulk of the inner cortex is composed of small-celled parenchyma but, scattered among this, there are a number of groups of thick-walled cells with dark contracted contents (Text-fig. 6). The middle cortex consists of larger, somewhat thick-walled, cells many of which, like the similar groups in the inner cortex, possess dark contents (Pl. 56, fig. 2). These thick-walled cells merge into a well-defined parenchymatous outer cortex of cells larger than those of the inner cortex enclosed by the small-celled epidermis. The surface of the stem, especially at and near the apex, bears numerous hairs. These are pointed and predominantly uniseriate though occasionally they possess a stouter multicellular base (Text-figs. 7*a*–*g*). They are present also on the basal parts of the petioles but do not appear to extend on to the more distal parts of



FIGS. 1–4. Camera lucida drawings of four transverse sections showing a two-fifths spiral sequence of monarch petiole traces. Figs. 1–3 show three stages in the emission of a reduced lateral outgrowth (*ro*). The petiolar bundles are numbered in the order of their development. All × 15. B.M. (N.H.) Holden Coll., slides H.92, H.153, H.177, H.192.

these. The actual stem apex is roofed in by a closely set mantle of these hairs which acted, presumably, as a protective cover for the delicate underlying tissues.

Two specimens of the stem in which the stele shows an equal dichotomy have been noted. The better example of this condition is that shown in Slide No. 549*c* and figured by Kidston (1908, fig. 6).



FIGS. 5, 6. Fig. 5, Transverse section of part of the stem stele near its apex showing the incompletely differentiated metaxylem and an isolated mesarch protoxylem tracheid. B.M. (N.H.) Oliver Coll. 1247. × 80. Fig. 6, A small group of dark sclerized cells from the inner cortex of the stem. Gordon Coll., King's College. × 80.

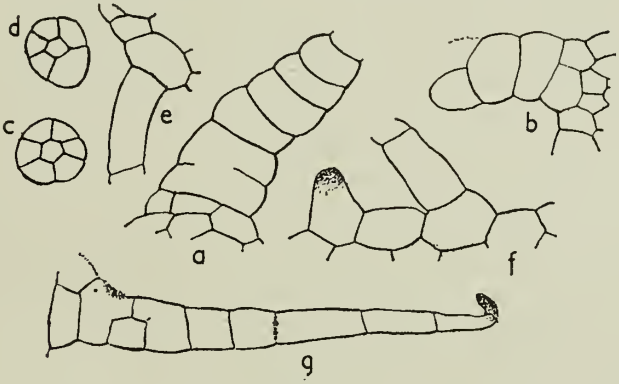


FIG. 7. Hairs from the stem and the base of the petiole. *a–d*, Kidston Coll., Glasgow University, slide 549*c*; *e–g*, Hemingway Coll., B.M. (N.H.) No. V.35555 (sections 35, 52 and 98 respectively). All × 135 approx.

The Petiole

As has been stated already, the petioles arise from the stems in a close spiral and usually show an approximately two-fifths divergence (Text-figs. 1–4). In the great majority of specimens the xylem and cortex are the only tissues preserved and even these may show some degree of breakdown. In the case of the xylem the protoxylem is the only part affected but the cortical tissues may become disorganized and, partly or almost wholly, be replaced by aggregates of calcite. These have crushed and ruptured the cortical cells and produced a pseudo-cellular structure in which the sphaerules of calcite have become surrounded by the broken down cell remnants (Pl. 57, fig. 6). This condition is not uncommon in petrified plant remains from Burntisland and was noted and figured by Gordon in some of the specimens of *Diplolabis* examined by him (Gordon, 1911).

The protoxylem of the petiole trace is initially mesarch with a single protoxylem group situated close to the adaxial surface. This mesarch position of the protoxylem persists for a short time after the separation of the trace from the stem stele but endarchy is usually attained by the time the petiole is free from the stem. The petiole trace is ovoid in transverse section with the spirally thickened protoxylem tracheids forming a distinct adaxial ridge (Pl. 56, fig. 1). Quite commonly, however, the protoxylem tracheids show partial or more or less complete disintegration and either are not preserved at all or are represented by dissociated fragments of the spiral thickening. An example of this latter condition is shown in Pl. 58, fig. 1, from a longitudinal section in the Figured Slide Collection of the Botany Department, Glasgow University. It is this variation in the degree of preservation of the protoxylem which probably accounts for the differing descriptions of Kidston (1908), Benson (1911) and Surange (1952). It seems evident that the small tracheids described by Kidston as protoxylem are in fact metaxylem elements and that the median groove described by Benson as situated in the centre of the protoxylem group is due to the loss of the spirally thickened tracheids forming the apex of the protoxylem ridge. The occurrence of this groove is relatively infrequent and is, in no sense, a characteristic feature of the trace. I am thus in agreement with the description of Surange who correctly describes the character and position of the protoxylem. The narrower metaxylem tracheids show scalariform thickening. Most of the metaxylem, however, the tracheids of which are much larger in diameter than those of the stem, possess two or more rows of transversely elongated pits (Pl. 58, fig. 1). Occasionally, traces of the phloem and its associated parenchyma are preserved but these are usually too small in amount to yield much information. The best preserved example so far discovered is that illustrated in Pl. 58, fig. 4, in which a strip of sieve tubes and phloem parenchyma occurs on the abaxial side of the vascular bundle. The endodermis consists of small, tangentially flattened thin-walled cells devoid of thickening and which may have dark contents. The inner cortex consists of parenchymatous cells, some of which may have been secretory in character. The latter are distributed singly through the rest of the parenchyma and are distinguished by their brown contents (Pl. 58, fig. 5). They bear a close resemblance to the mucilage-secreting cells commonly occurring in the cortex of many existing ferns. The cortical cells diminish in size towards the exterior and, in mature petioles, these smaller cells develop thickened walls and form a well-defined sclerenchymatous outer zone. The small-celled epidermis shows no specially distinctive features, apart from the uniseriate surface hairs developed at and near the bases of the petioles. The branching of the petiole follows no set pattern and the examples figured by Surange (1952) adequately illustrate its general character. The branches undergo progressive diminution in size and may undergo, occasionally, equal bifurcation near their junction with a branch of a higher order, as in the example shown in Pl. 60, fig. 5.

Associated with the vascular bundles which supply the petioles are much smaller monarch traces supplying the organs which Benson termed aphlebiae and which she described as uninerved sheathing organs. According to her, the monarch petiolar bundles " apparently never come off (*from the stem stele*), pass through the cortex and enter the petiole without being accompanied by aphlebiae ". Surange, although describing and figuring one of these small monarch bundles as being given off from the stem stele immediately following the emission of the first petiole trace (Surange, 1952, text-fig. 1, *c–f*) does not record or figure them as constantly accompanying subsequent petiole traces. The sections studied during the present investigation do not support the view that they accompanied all, or indeed the majority, of the petiole traces. Where they are present, their relation to these traces is very variable and the two examples figured here show a wide divergence in their point of origin from the stem stele. The first, illustrated in Pl. 56, fig. 1 and Text-figs. 1–3, arises quite independently as a small endarch trace between the first and second of the petiole traces figured and is approximately equidistant between them. It ultimately supplies a small outgrowth of the stem which is ovoid in transverse section with the flatter side adaxial. The two examples illustrated by Benson (1911, text-figs. 1*a*, *b*) appear to supply similar outgrowths. Both are from thick and somewhat poorly preserved sections but that shown in her text-fig. 1*a* clearly shows the beginning of the ovoid shape in transverse section which is assumed when the " aphlebia " becomes free from the stem cortex. The second example (Benson's text-fig. 1*b*) appears to be more closely associated with an outgoing petiole and has an irregular shred of cortical tissue linking it with this. As in her text-fig. 1*a*, there are indications that, in this example also, the " aphlebia " was ovoid and not winged in transverse section.

The second example figured in the present paper is one in which the vascular bundle destined for the petiole and that destined for the small monarch trace arise simultaneously from the stem stele and are initially completely fused. As the petiolar trace passes into the stem cortex the small bundle becomes independent and diverges from the larger one though it accompanies it into the petiole (Pl. 56, figs. 1, 2). Whether this bundle should be interpreted as an abortive " aphlebia " or a precocious branch of the petiole is a matter of opinion. It should be pointed out, however, that a complete series exists ranging at the one extreme from a strand arising from the stem stele without any obvious connection with that supplying the nearest petiole to that just described in which the linkage between the two is close and prolonged.

Whatever the interpretation of the morphological nature of the structures supplied by these strands may be, they differ widely from the type of structure to which Solms-Laubach (1891) applied the descriptive name " Aphlebia ". This was applied by him to a distinctive and anomalous type of pinna or pinnule possessing a reduced and deeply dissected lamina which occurred on the rachises of certain fossil ferns and pteridosperms. These were compared by him to similar pinnae present in *Hemitelia capensis* and other existing ferns. Subsequent authors have applied the name to the scale-like structures occurring on the stems of several of the zygopterid ferns and to the somewhat similar pinnules borne on their petioles (Potonié, 1903 ; Seward, 1910 ; Bertrand, 1911 ; Gordon, 1911 ; Scott, 1920). This extended use of the name " Aphlebia " does not appear to serve any really useful purpose and it would seem preferable to limit it to the type of structure to which Solms-Laubach originally applied it.

The Diarch Axes

In addition to the monarch petioles, there were other, generally stouter, axes possessing two adaxial protoxylem groups, which were obviously parts of the same plant. These, as already stated, were regarded by Benson (1911) as diarch petioles but have been interpreted provisionally by Surange (1952) as dorsiventral stems from which the radially organized plants arose. We owe the detailed description of the development of these radially organized plants from the diarch axes to Surange and, apart from minor details, there is little to add to his account of the specimens he studied. A typical specimen, cut obliquely and showing two stages in the formation of a radial stem, is illustrated in Pl. 56, figs. 3, 4. It is evident that Benson's material was inadequate for a similarly detailed study and this led her to misinterpret the sections figured in her paper as " successive transverse sections through a stem stele " (Benson, 1911, pl. 81, figs. 1–5).

Re-examination of the relevant slides in the Benson Collection leaves little doubt that they represent part of a diarch axis from which a radial stem is developing. The section figured by Kidston (1908, fig. 11) and described by him as that of a petiole showing an early stage in petiolar dichotomy is also probably one of a diarch axis showing an early stage in the development of a radial stem.

Whilst, however, both the Benson and Kidston specimens described above fit without difficulty into Surange's interpretation of the behaviour of the diarch axis this interpretation is unsatisfactory when applied to the specimen figured by Benson (1911, pl. 82, figs. 11–13, 11*a*–13*a*). In the sections from which this series of figures has been made there is no indication that the diarch axis has divided into two monarch daughter axes, one of which is destined to be the source of a radial stem. The figured sections are interpreted by Benson as " a series through a stem bearing at first a diarch trace and later roots ". She also states that " the series shows diagrammatically the change in character of the stem as it passes from a purely leaf-bearing zone into a root-bearing zone ". The sections upon which this interpretation is based are the second, third and fourth of a series of five slides numbered 417·1 to 417·5, figs. 11 and 11*a* showing the stage present in 417·4, figs. 12 and 12*a* that present in 417·3 and figs. 13 and 13*a* that present in 417·2. Of the two remaining slides in this series 417·5 shows no substantial change from that in 417·4 and 417·1 has been shattered during grinding. A comparison of Benson's pl. 81, fig. 2 with her fig. 11*a* shows that these are essentially similar and it is suggested that both represent an early stage in the development of a radial stem. Whereas, however, the plant illustrated in her figs. 1–5 fits in with Surange's account of the behaviour of the diarch axis that illustrated in the 417 series clearly differs since the radial stem originates on one side of this axis without involving its division into two monarch daughter axes.

In addition to the Benson Collection specimen, there is a relatively short series of " peels " in the author's collection which presents some difficulties of interpretation when considered in connection with Surange's views. This series consists of ten transverse sections numbered H.96 and H.103 to H.111 and ten longitudinal sections through the base of the specimen numbered H.112 to H.121. A typical transverse section shows a well-developed diarch axis linked with the stem by its cortical tissues (Pl. 59, fig. 1). The stele of this axis unites with that of the stem at a lower level and is well shown in slide number H.115 (Pl. 59, fig. 2). This slide, owing to the curvature of the specimen, shows the axis and the stem partly in transverse and partly in longitudinal section. The stem stele is clearly radial in type but the series is unfortunately too short to yield any information as to its origin. On the opposite side of the stele to that at which fusion with the diarch axis has occurred there is a large developing lateral trace occupying almost two-thirds of the area of the stele. The stem cortex consists almost entirely of thick-walled cells and only towards the lower transverse sections is there any indication of root development though at this level two root traces are coming off in close juxtaposition. Whether or not this specimen is one of a stem from which two successive diarch axes have been produced must be an open question but if this interpretation is accepted it provides some support for the view put forward by Benson as to the plant being heterophyllous. It certainly differs to a marked extent, both in the nature of its cortical tissues and in its stelar characters, from a typical radially organized stem.

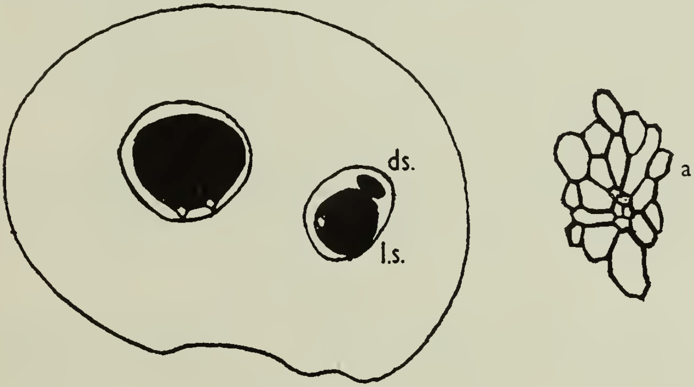


Fig. 8. Camera lucida outline of a diarch petiole in transverse section which has given off a lateral strand (*ls*) and which in its turn has given off a daughter stele (*ds*). Fig. 8*a*, Daughter stele, × 150. B.M. (N.H.) Oliver Coll. 1272.

An additional and different type of behaviour is also shown by some diarch axes which produce lateral branches having no apparent connection with radial stem formation. Benson (1911 : 1048) refers to a specimen of this kind (Benson Collection, Series 390) and figures an early stage in the formation of such a lateral branch (pl. 83, fig. 24). These branches are initiated by the division of one of the two protoxylem groups of the diarch axis following which the outer protoxylem group, together with its associated metaxylem, separates off to form the branch trace. Three of the stages in the formation of such a branch are illustrated in Pl. 57, figs. 4–6, from slides in the Oliver Collection. In an additional section at a stage similar to that in Pl. 57, fig. 6, the lateral trace has, in its turn, developed a small, somewhat irregular group of tracheids on its abaxial side which suggests that it may be possibly an early stage in the formation of a stem (Text-figs. 8, 8*a*). Any firm view as to its significance, however, is impossible on the evidence of an isolated section and it is figured here primarily to record its existence.

The specimens studied by Surange (1952) gave no clue to the origin of the diarch axes and it was clearly important to ascertain this, if possible, before any assessment could be made of their morphological status. Before attempting this, however, it seemed desirable that a review of the evidence upon which Surange had based his interpretation should be made. He, himself, realized that he had to rely on the criteria provided by comparative anatomy and that the acceptance of his view presented certain difficulties. Some of these, such as the pseudocollateral vascular structure, the possession of tracheids of wide diameter similar to those of the monarch petioles and differing from those of the radial stem and the fact that the axes do not appear to develop either petioles or a root system, were noted by him. In support of his view, however, he points out that among the Hymenophyllaceae the stems of certain species such as *Hymenophyllum sericeum* possess a pseudocollateral type of vascular structure closely resembling the condition present in the diarch axes of *Botryopteris antiqua*. It is doubtful, however, how much weight can be given to this comparison since *Hymenophyllum sericeum* is one of a series of filmy ferns in which there is a progressive reduction in the amount of vascular tissue this consisting, in the ultimate members of the series such as *H. tunbridgense*, of a minute pseudocollateral monarch strand (Boodle, 1900 ; Tansley, 1908 ; Ogura, 1938).

There does not seem to be any evidence that *Botryopteris antiqua* was a species in which reduction of the vascular system had occurred and it is suggested that a study of the anatomy of the stem and leaf stolons characterizing certain living ferns would provide a closer analogy with the diarch axes of *B. antiqua* than that used by Surange.

Among the ferns developing stem stolons those which have been most extensively studied are various species of *Nephrolepis* (e.g. *N. exaltata*, *N. cordifolia*, *N. neglecta*) (Lachmann, 1885, 1889 ; Sperlich, 1906 ; Sahni, 1916) but Bower (1923, 1926) also records their occurrence in *Plagiogyria pycnophylla* and *Thyrsopteris elegans*. In all these ferns the symmetry of the vascular supply of the stolon is radial in type and, initially at least, is a simplified version of that of the stem of the parent plant. The ferns in which flagelliform leaf stolons are developed are among those which have been investigated by Kupper (1906) in his comprehensive study of the formation of sporophytic buds on the leaves of ferns. Among these there is a group of related species of small fern belonging to the genus *Asplenium* namely *A. obtusilobum* Hk., *A. lauterbachii* Christ and *A. mannii* Hk. The first of these three species in addition to the normal leaves produces a series of transitional forms showing progressive reduction in the number of pinnae (Text-figs. 9*a*, *b*) the ultimate members being flagelliform stolons in which no pinnae at all are produced. These stolons and the modified leaves in which the pinnae are reduced develop sporophytic buds at intervals and are apparently of unlimited growth. Material of *A. obtusilobum*, a species from the New Hebrides, and of *A. lauterbachii*, from New Guinea, was not available for study but through the good offices of Mr. N. C. Chase of Umtali, Southern Rhodesia, a good supply of *A. mannii* was obtained. The specimens were collected from the North Range of the Vamba Mountains where it grows as an epiphyte on the boles and branches of forest trees. These plants, in addition to the normal leaves, bear flagelliform stolons (Hooker, 1854) on which sporophytic buds in various stages of development are produced, the longest of these in the material sent by Chase measuring 35 cm. and bearing ten attached plantlets (Text-fig. 9*c*). It is hoped to make a detailed investigation of this species later but, in connection with the present paper, attention has been concentrated on the morphology of the bud-bearing stolons. The vascular supply of these stolons consists of a somewhat strap-shaped xylem strand surrounded by phloem and phloem parenchyma with a protoxylem group occupying each extremity of the trace (Text-fig. 10*a*). When a sporophytic bud is to be formed one of the protoxylem groups accompanied by a small amount of metaxylem is detached from the rest of the leaf trace and becomes linked with the vascular supply of the developing sporophyte (Text-figs. 10*b*, *c*). This condition appears to furnish a close parallel to the behaviour of the vascular bundle in the diarch axes of *Botryopteris antiqua* and suggests that, applying the criteria of comparative anatomy, these

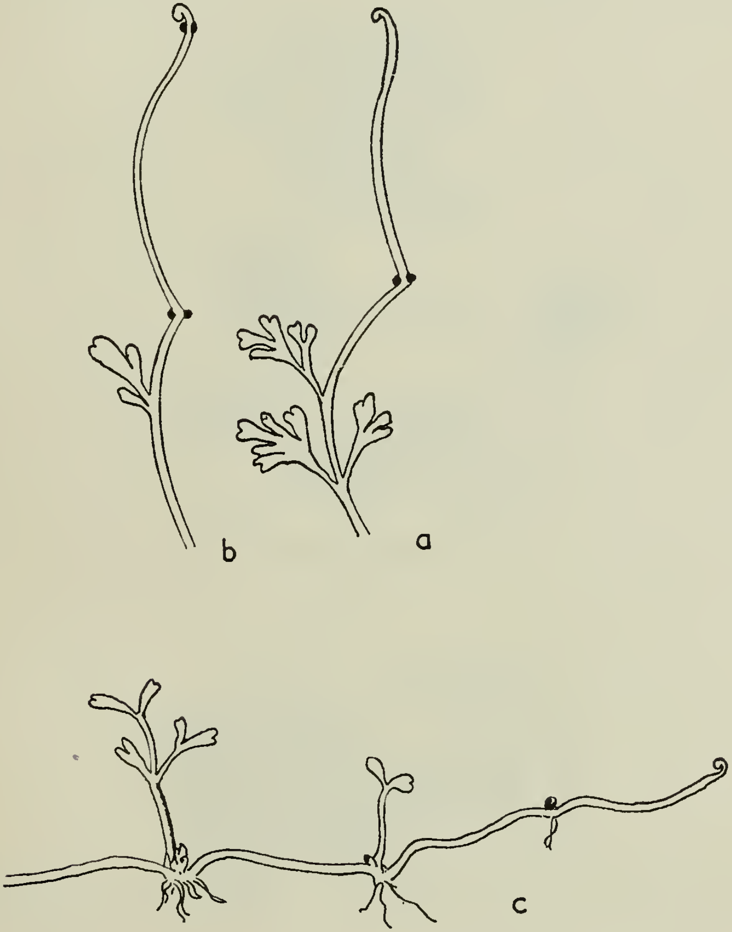


FIG. 9. *a*, *b*, Two leaves of *Asplenium obtusilobum* showing progressive pinna reduction and the formation of sporophytic buds. *After* Kupper, 1906. *c*, Part of a leaf stolon of *Asplenium mannii* showing three developing plantlets. All nat. size.

would be more accurately interpreted as specialized petioles rather than as dorsiventral stems. Whilst, however, on the criteria provided by comparative anatomy, there seem to be reasonable grounds for interpreting the diarch axes as petioles rather than stems it was considered that a search for specimens showing their origin was essential and several of the slides in both the Oliver and Gordon Collections yielded useful information in this connection. Two of the slides from the Oliver Collection (Pl. 57, figs. 2, 3) are from consecutive sections numbered 1263 and 1264 and show two successive stages in the departure of a typical diarch strand. This diarch strand and that illustrated in Text-fig. 11*a* arise from stems which appear to be radial in

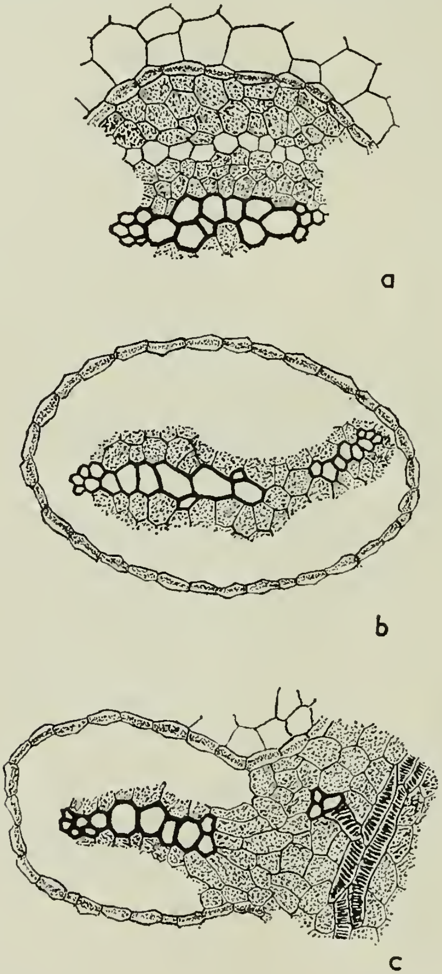


FIG. 10. Transverse sections of a leaf stolon of *Asplenium mannii* showing the development of the connection between the vascular bundle of the stolon and that of the sporophytic bud. × 170.

type. That these are, in fact, successive stages in its departure is shown by an examination of the next slide in the series (No. 1265). The stem and petioles in this slide are badly disintegrated but the xylem of the stem stele is intact and in it the differentiation of the xylem is still incomplete. It is interesting to note that this stem does not show a close succession of spirally developed monarch strands. In the section shown in Text-figs. 11*a*, *b*, however, a much smaller double vascular bundle has come off from the stem stele almost at right angles to that from which the diarch strand has arisen. This smaller bundle appears to be the vascular supply of a monarch petiole and is composed of two unequal endarch xylem groups (Text-fig. 11*b*). It bears a close resemblance to those strands already described in which the main petiolar strand is accompanied by a smaller accessory strand. Of the three slides from the Gordon Collection which are figured, two (Pl. 57, fig. 1 and Pl. 58, fig. 3) show a large diarch strand, with two mesarch protoxylem groups, lying in close proximity to the radially organized stem stele. In the third (Pl. 56, fig. 2) a similar

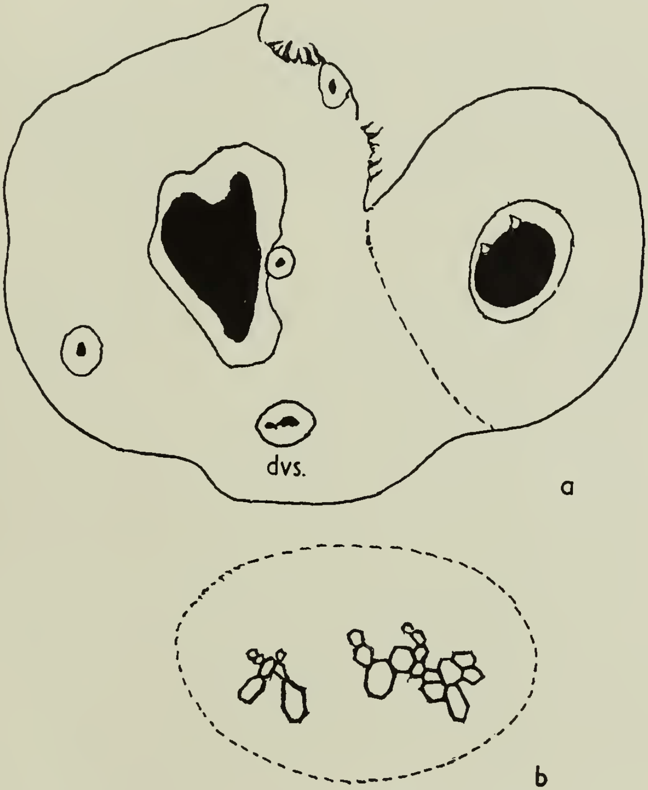


FIG. 11. *a*, Camera lucida outline of an oblique stem section showing an attached diarch axis and a small double vascular strand (*dvs*); *b*, the double vascular strand more highly magnified. B.M. (N.H.) Oliver Coll. 1274. *a*, ×30; *b*, ×150.

large diarch strand with mesarch protoxylems is dividing into a larger and a smaller bundle though these are still united. They show a pronounced difference from those cases in which a monarch petiolar strand is associated with a much smaller one. It is suggested that the dividing mesarch strand in this Gordon specimen may represent an unusually early division of the diarch axis prior to the formation of a radial stem from the smaller bundle. Like the specimens from the Oliver Collection, none of the Gordon specimens shows any indication of a close succession of spirally arranged monarch petioles.

It would seem fair to sum up the evidence as to the nature of the diarch axes by stating that the data provided by comparative anatomy and the evidence yielded by newer discoveries among the specimens of *Botryopteris antiqua* itself favour the interpretation of the diarch axes as petioles and that their development leads to a pronounced modification in the emission of the monarch petiole traces though there is no convincing evidence that the monarch and diarch petioles were developed in alternating series.

The Root System

The adventitious root system is mainly composed of slender diarch roots which show a close measure of structural agreement with those of existing leptosporangiate ferns. They possess a separate cortex from their point of origin with the stem stele and, in this region, the xylem is bulkier than it is in the more distal parts thus forming an expanded base of attachment (Pl. 56, fig. 2). The phloem and its associated parenchyma and most of the parenchymatous inner cortex are seldom preserved. In the few cases where it has survived petrifaction the inner cortex has, scattered through it, an irregular ring of cells with dark contents similar in type to those present in the inner cortex of the petiole (Pl. 56, fig. 3). The endodermis, also like that of the petiole, is formed of small tangentially flattened cells which often have dark contents. The outer cortex consists of thick-walled cells, smaller than those of the inner cortex, these forming a zone several cells in depth (Pl. 56, figs. 3, 4). As a rule, the surface layer of the roots has been eroded but even when this has survived no evidence has been found of the existence of root hairs.

In addition to the roots of the type just described, there are others which appear to be most abundant towards the stem apex and which show pronounced morphological differences from these. The evidence for the existence of this second type of root was initially somewhat unsatisfactory as their morphology was obscured by partial collapse and distortion. Happily, among the plants from a block in the Hemingway Collection a stem occurred which had developed a number of uncrushed roots thus enabling their salient features to be determined. There appears to be no doubt that these organs are roots since, like those already described, they possess their own cortex from the time of their inception and their xylem consists of a small diarch plate with an exarch protoxylem group at each end (Pl. 60, figs. 2, 3). The stele is relatively small and is surrounded by a wide cortex composed entirely of parenchyma, the cells of which have dense finely granular contents especially in the immature region near the apex (Pl. 60, figs. 1, 2). The surface layer is formed of dark flattened cells in which no detailed structure can be discerned (Pl. 60, figs. 1–3).

Any attempt to indicate the function of these roots must be somewhat speculative although their origin near the upper end of the stem and their morphology both suggest the possibility that they may be aerial and perhaps assimilatory in character.

Sporangia and Spores

Our knowledge of the sporangia and spores of *Botryopteris antiqua* is the least satisfactory part of the information available about this Lower Carboniferous plant though one can assign these to it with some degree of probability. The most satisfactory evidence yielded so far is that produced by Surange though even this is by no means conclusive. Commonly associated with the stems and petioles are sporangia with a multiseriate annulus, some of which contain well-preserved and quite distinctive spores. These sporangia are apparently borne on slender, branching axes each of which is traversed by a delicate vascular strand and the epidermis of which is characterized by dark cell contents. These have contracted away from the cell walls in many instances giving them a readily recognized appearance, especially in surface view (Pl. 60, fig. 6). The slender branches are closely associated with small branches of *Botryopteris antiqua* petioles which also often have epidermal cells with dark contents (Pl. 60, fig. 7). The spores contained in the sporangia are triangular in plan and are somewhat flat with trilete rays extending about three-quarters of the way towards the margin of each radius. They are smooth-walled and devoid of any ornamentation. The radial extremities are rounded and the interradial margins are concave. In proximal view the spores show a narrow raised margin but when seen from the distal side they show three large equal lobes surrounding a central triangular depression which leads to a flat, partly enclosed, central area (Text-figs. 12*a–c*). They are identical with those filling the sporangia which Scott (1910) figured and described and which he regarded as possibly those of *B. antiqua*.

Careful and detailed descriptions of palaeozoic spores are a relatively recent feature of palaeobotanical studies and already palynology has produced a considerable specialized literature with regard to them. The earliest reference to spores with a triangular contour which has been traced so far is one by Renault (1896). His figure 17 shows a sporangium termed by him *Hymenophyllites β* in which most of the spores are spherical but in which there are also some spores which are triangular (*trigones*). In Renault's view (1896 : 20) it is probable that this appearance is due to a partial desiccation of the spores.

Recent investigations, however, have shown that subtriangular types of spore occur quite commonly among palaeozoic spore assemblages. Among these Kosanke (1950, pl. 3, fig. 4) illustrates a spore of this kind to which he has given the name *Granulosporites concavus*. This has rounded corners, is smooth-walled and has strongly concave margins between the radii. Mamay (1950) also lists a species, *Botryopteris illinoensis*, which, like Kosanke's material, is from the Pennsylvanian of Illinois and in which the spores are described as " axially flattened, triangular, with concave sides " (Mamay, 1950, pl. 2, fig. 9).

These spores are from more recent geological strata than that in which *Botryopteris antiqua* occurs but spore assemblages from parts of the Scottish Lower Carboniferous have recently been investigated by Butterworth & Williams (1958) and by Love

(1960). Both these authors have described isolated spores which appear to show a close resemblance to those associated with *B. antiqua*. These were assigned by Butterworth & Williams to the genus *Granulosporites* as *G. politus* but by Love to *Leiotriletes politus*. Love very kindly loaned to the Department of Palaeontology a " single spore " slide of his *Leiotriletes politus* for comparison with the spores present in the sporangia from the Calciferous Sandstone and this has established beyond reasonable doubt that this spore and the spores from the petrified sporangia are identical.

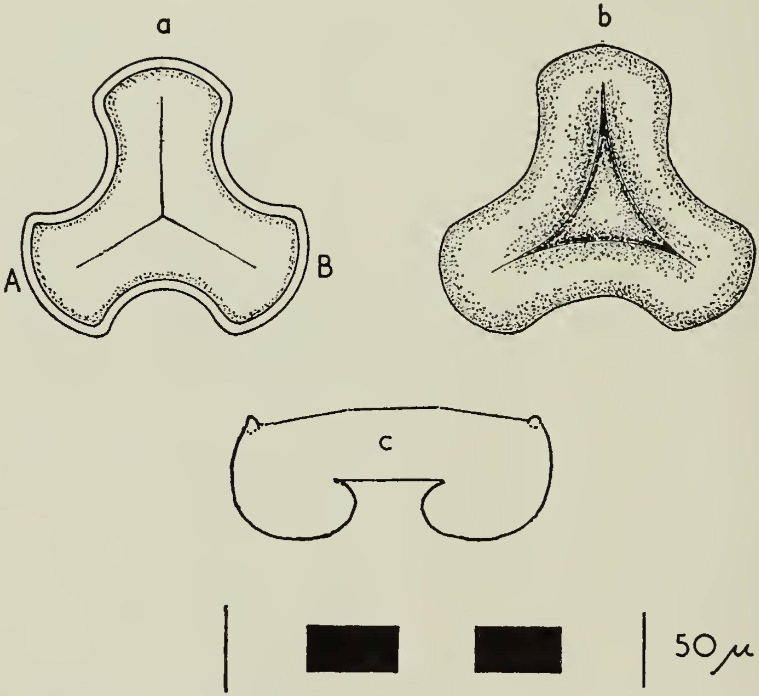


FIG. 12. *a*, Proximal and *b* distal appearance of trilete spores ; *c*, section of spore along plane A, B, of 12*a*. *a*, Surange Coll. B.154 ; *b*, Surange Coll. B.70

The evidence for the assigning of these sporangia and spores to *Botryopteris antiqua* is obviously not conclusive and it is hoped that proof of their relationship will be furnished when suitable specimens are available.

Neither Kidston, Benson nor Surange have attempted a formal diagnosis of *Botryopteris antiqua* and the following is suggested as covering the known data :

Botryopteris antiqua Kidston

DIAGNOSIS. Small palaeozoic fern. *Stem* radially organized, protostelic with wholly tracheidal xylem, narrow scalariform tracheids forming bulk of stele, often wider tracheids with two or more rows of transversely elongated pits developed peripherally;

protoxylem spirally thickened ; mesarch : cortex divided into parenchymatous inner and outer zones with sclerenchymatous middle zone ; epidermis, especially at and near stem apex, developing numerous unbranched uniseriate hairs forming a protective mantle over the apex and extending on to bases of petioles. *Petioles* oval in transverse section, monodesmic with initially mesarch protoxylem becoming endarch ; petioles of two kinds, one possessing a single adaxial protoxylem group, the other possessing two adaxial protoxylem groups ; monarch petioles developed in close spiral succession, branching repeatedly, sometimes accompanied by small endarch subsidiary vascular bundle ; diarch petioles often developing sporophytic buds giving rise to radially organized daughter plants and, when present, largely replacing monarch petioles. *Roots* diarch with separate cortex throughout. majority with sclerenchymatous outer cortex. A second type of root with wide, wholly parenchymatous cortex developed at and near stem apex.

Sporangia provisionally assigned to *B. antiqua* having a multiseriate annulus and containing subtriangular, smooth-walled and trilete spores with rounded angles and concave interradii.

LECTOTYPE.—A transverse section of a dichotomizing stem figured by Kidston (1908, fig. 6) bearing roots and a petiole. Kidston Coll., Glasgow University, slide 549*c*.

DISCUSSION

It is almost inevitable that the study of the morphology of any fossil plant is one which shows a progressive series of stages largely dependent on the number and quality of preservation of the specimens available to the investigator and, to a less extent, on the evolution of techniques which enable a better use to be made of those at his disposal. The series of morphological studies of *Botryopteris antiqua* including the present paper clearly exemplify this. Although the plant was first recognized and briefly described by Kidston the chief value of his paper was that it provided a basis for further study. Benson's work appreciably amplified our knowledge though the techniques then available led her to misinterpret some of the plant's morphological characteristics. Surange, applying newer techniques, has been able to correct certain of these misinterpretations and to make appreciable additions to our knowledge though some of his tentative interpretations have oversimplified the morphological problems involved. These three investigators have provided, however, a reasonably secure foundation for further work and it is considered that the present account simply marks an additional stage in the elucidation of the morphology of this palaeozoic fern. The most important feature about which additional information is desirable is definite proof that the associated sporangia are those of *Botryopteris antiqua*. More detailed knowledge of the behaviour of the diarch petioles would be welcome also. Their preservation mainly as comparatively short, isolated segments fails to give a clear idea of their complete morphology. This may be due to their being shed from the parent plant when mature or by their being parted from it by decay of the parts connecting one with the other. The radially organized plants to which they give rise vary considerably in size but this may well be due to the stage of development they have reached. They are obviously not terminal in position but the minute stele figured in Pl. 59, fig. 7, which, though fully differentiated, only measures 0·3 mm. in diameter probably developed from the distal part of the parent axis. Quite small petioles with steles having two symmetrically placed adaxial protoxylem groups are not uncommon but whether they represent the initial stage in the branching of a monarch petiole or the distal parts of a diarch petiole cannot be determined from isolated sections.

Botryopteris antiqua seems to fall naturally into place taxonomically among the European Coal Measure species of the genus though its petiolar anatomy is somewhat simpler. It shares with them a homogeneous protostele with mesarch protoxylem groups, the apex of which is protected by predominantly uniseriate unbranched hairs and a monodesmic petiolar vascular supply which retains the form of a tangentially compressed cylinder. It also shares with *Botryopteris hirsuta* the specialized type of petiole on which sporophytic plantlets are developed. Whether the genus *Botryopteris* as at present constituted is a natural one is perhaps open to some doubt. *B. forensis* and some of the American species such as *B. americana* (Delevoryas & Morgan, 1954) and *B. trisecta* (Mamay & Andrews, 1950) have much in common and show considerable differences from the European Coal Measure species and from *B. antiqua*. The best solution, if all are to be retained in the same genus, would seem to be the creation of separate subgenera for the two groups.

SUMMARY

Botryopteris antiqua is a minute fern occurring in the Scottish Lower Carboniferous.

The stem, which is radially organized, possesses a stele which has the shape of a shallow dome. It is protostelic with xylem which is wholly tracheidal and in which the protoxylem is mesarch. The xylem is enclosed by a continuous sheath of phloem and by a cortex differentiated into parenchymatous inner and outer zones and a sclerotic middle zone. The stem apex is overarched by a closely set system of unbranched and predominantly uniseriate hairs which extend on to the proximal parts of the petioles.

These are of two kinds, monarch with a single adaxial protoxylem and diarch with two adaxial protoxylem groups. The petiolar vascular supply is monodesmic and has the form of a tangentially flattened cylinder with the protoxylem forming either one or two adaxial ridges. The monarch petioles branch freely and are developed in spiral succession.

The diarch petioles are generally larger than the monarch ones and branch less frequently. They often produce sporophytic buds and their development interrupts the spiral development of the monarch ones.

The root system consists of diarch roots of two kinds, the majority having an outer zone of cortical sclerenchyma. In a second type of root the cortex is wholly parenchymatous.

Sporangia which are frequently associated with the stems and petioles have a multiseriate annulus and contain smooth-walled subtriangular trilete spores with concave interradii.

ACKNOWLEDGEMENTS

In addition to those whose help has been acknowledged in the body of the paper, the author is also greatly indebted to Dr. E. I. White, Keeper of the Department of Palaeontology, for facilities for studying the palaeobotanical collections in his charge, to Mr. F. M. Wonnacott for his expert help in many ways and to the staff of the Photographic Department of the Museum for their care and co-operation in the production of the negatives and prints from which the plates illustrating this paper have been made.

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PLATE 56

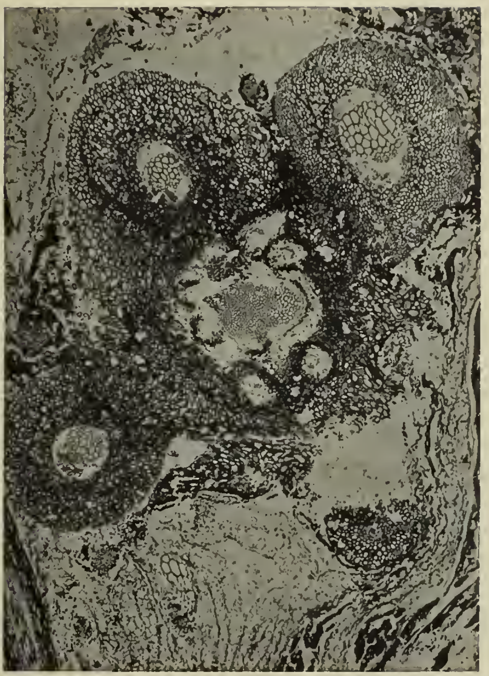
Botryopteris antiqua Kidston

FIG. 1. Transverse section of a stem showing stages in the emission of petioles and root traces. Note the sclerized outer cortex of the roots and, at the right bottom corner of the figure, one of Benson's " aphlebiae ". B.M. (N.H.) Holden Coll., No. H.152. × 12.

FIG. 2. Transverse section of stem in which the whole of the cortical tissues are preserved and which shows the emission of three roots and a dividing petiole trace with mesarch protoxylems. Gordon Coll., King's College, London. × 12.

FIG. 3. Oblique section of a dividing diarch petiole, the smaller branch of which is associated with the basal root-bearing part of a daughter sporophyte. Note the increase in the number of tracheids where the root steles join the parent stele. B.M. (N.H.) Holden Coll., No. H.152. × 12.

FIG. 4. Oblique section of the same plant as that shown in Fig. 3 but cut at a lower level and in which the daughter stem is well shown. B.M. (N.H.) Holden Coll., No. H.162. × 12.



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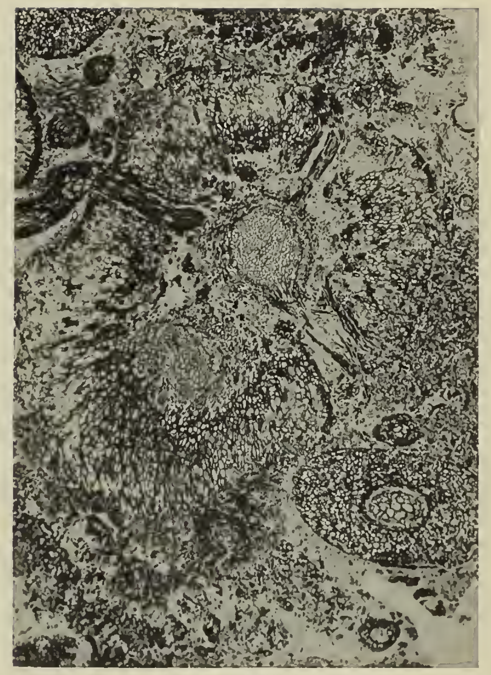

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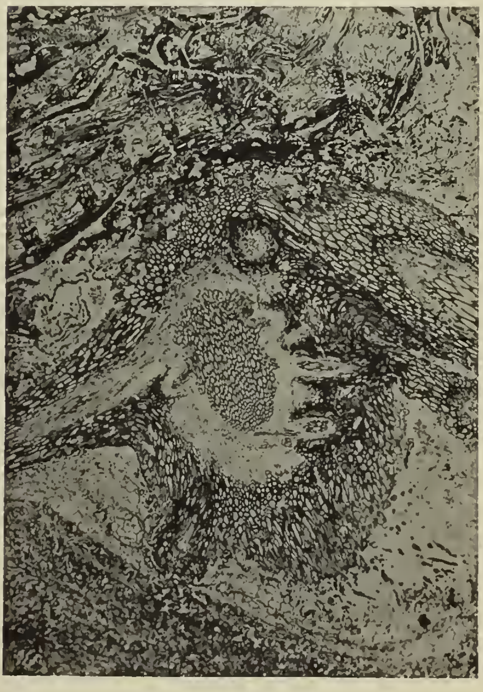

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BOTRYOPTERIS

PLATE 57

Botryopteris antiqua Kidston

FIG. 1. Transverse section of a stem with a large mesarch petiole trace with two protoxylem groups. The cortical tissues are well preserved and the small-celled epidermis is clearly shown on the lower side of the figure. Gordon Coll., King's College, London. × 10.

FIGS. 2, 3. Transverse sections showing two stages in the emission of a diarch petiole. Fig. 2, B.M. (N.H.), Oliver Coll., No. 1263 ; Fig. 3, Oliver Coll., No. 1264. × 10.

FIGS. 4–6. Sections showing three stages in the emission of a branch trace from that of a diarch petiole. B.M. (N.H.) Oliver Coll., Nos. 1261, 1262, 1238 respectively. All × 15 approx.


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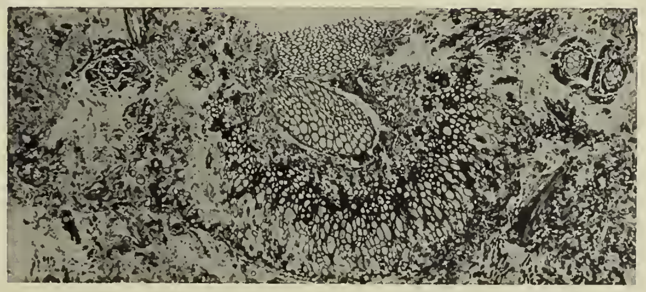
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BOTRYOPTERIS

PLATE 58

Botryopteris antiqua Kidston

FIG. 1. Longitudinal section of part of the xylem of a petiole showing the types of tracheidal pitting and the disruption of the protoxylem. Glasgow Univ. Figd. Slide Coll., No. 714. ×150.

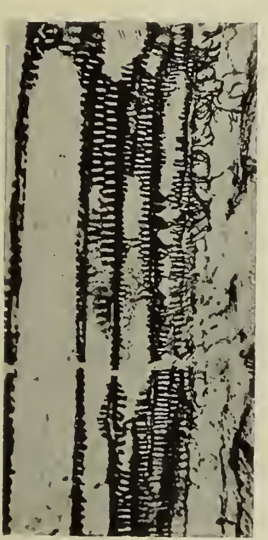
FIG. 2. Longitudinal section through the protoxylem of a petiole showing an early stage in the breakdown of the spirally thickened tracheids. B.M. (N.H.) Holden Coll., No. H.162. ×70.

FIG. 3. Transverse section of stem giving off a root trace and with a large petiole trace with two protoxylem groups to the left of the figure. Gordon Coll., King's College, London. ×16.

FIG. 4. Transverse section of a petiole showing a strip of sieve tubes on the abaxial side of the stele. Gordon Coll., King's College, London. ×35.

FIG. 5. Part of a petiole in both transverse and longitudinal section showing the cortical secretory cells. Surange Coll., No. B. 34. ×20.

FIGS. 6–8. Transverse sections of successive stages in the emission of a petiole trace and a subsidiary daughter trace. B.M. (N.H.) No. V.35555; Fig. 6, slide 73*b*; Fig. 7, slide 82*b*; Fig. 8, slide 86*b*. All ×20.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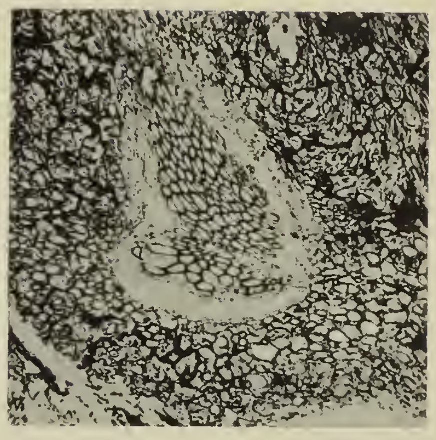
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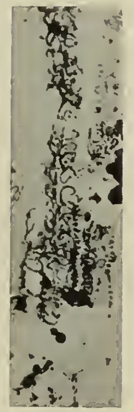
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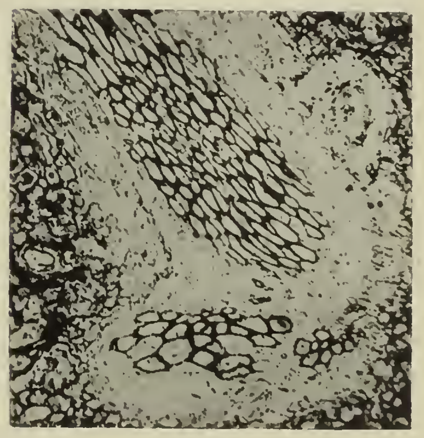
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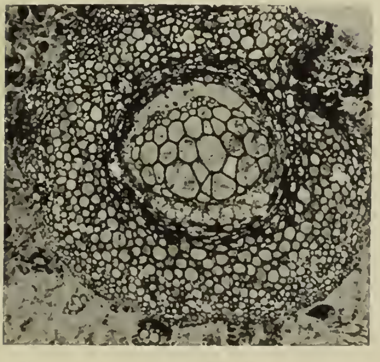
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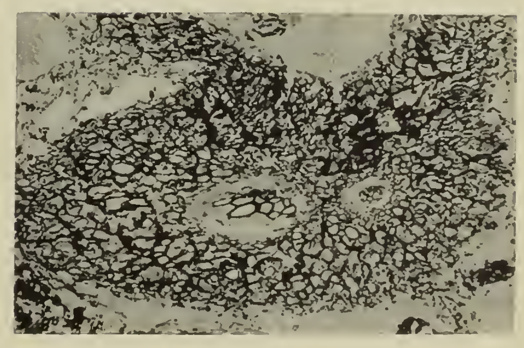
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BOTRYOPTERIS

PLATE 59

Botryopteris antiqua Kidston

Fig. 1. Transverse section of a stem with attached diarch petiole to the right and showing an early stage in the formation of a second petiole trace to the left. Note the character of the stem cortex. B.M. (N.H.) Holden Coll., No. H.101. × 16.

Fig. 2. The same stem cut partly in transverse and partly in longitudinal section showing the junction of the petiole trace with the stem stele. B.M. (N.H.) Holden Coll., No. H.115. × 16.

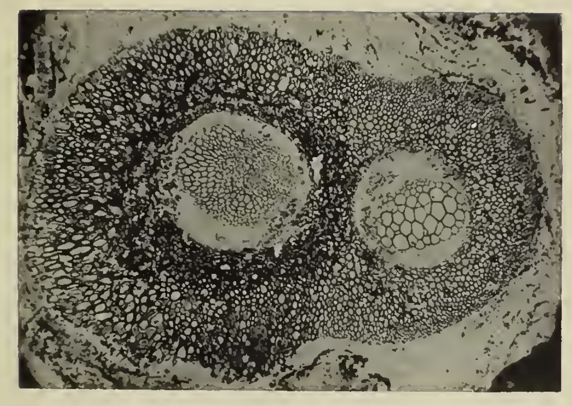
Fig. 3. Section through a stem showing a circinately coiled petiole and, to the right, parts of surface hairs. The small ringed group of xylem is much more highly magnified in Fig. 4. Surange Coll., No. B.78. × 20.

Fig. 4. Small group of tracheids showing a spiral protoxylem and a pitted metaxylem element. Surange Coll., No. B.78. × 700.

Fig. 5. Transverse section of an immature root still embedded in the stem cortex. Note the diarch xylem plate and the cortical cells with dark contents. Kidston Coll., Glasgow University, No. 670*c*. × 100.

Fig. 6. Transverse section of a stem stele near its apex showing incomplete differentiation of the xylem. Surange Coll., No. B.34. × 50.

Fig. 7. Transverse section of the stele of a very small stem in which the differentiation of the xylem is complete. B.M. (N.H.) No. V.35555, slide 3*b*. × 100.



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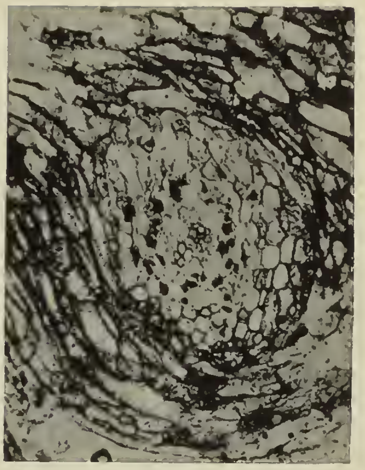

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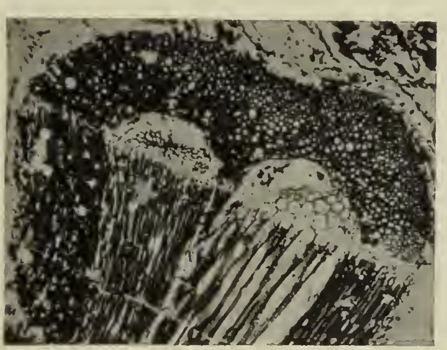

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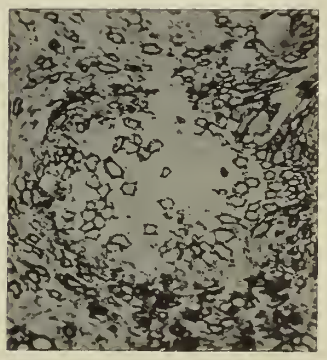

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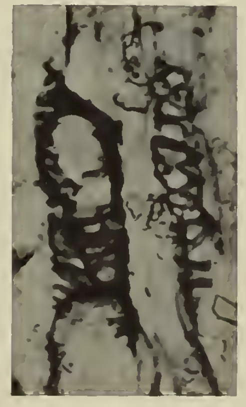

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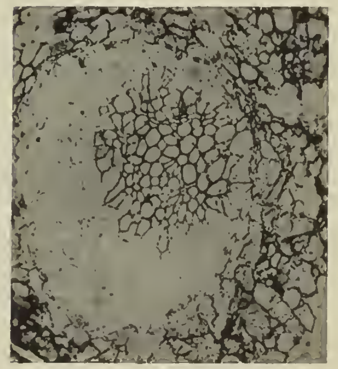


7

BOTRYOPTERIS

PLATE 60

Botryopteris antiqua Kidston

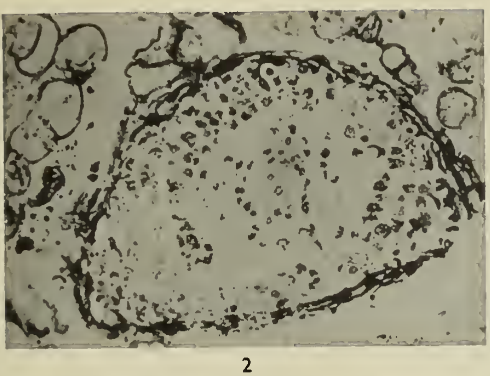
FIGS. 1–3. Successive stages in the differentiation of a second type of root. Note the dense contents of the cortical cells and the traces of surrounding hairs in Figs. 1, 2. B.M. (N.H.) No. V.35555. Fig. 1, slide 58*b* × 100; Fig. 2, slide 65*b* × 100; Fig. 3, slide 44*b* × 100.

FIG. 4. Transverse section of a petiole from Autun showing the characteristic adaxial concavity. Kidston Coll., Glasgow University, No. 2046. × 25.

FIG. 5. Transverse section of a branching petiole giving off two approximately equal daughter traces. Kidston Coll., Glasgow University, No. 1471. × 40.

FIG. 6. Minute sporangium-bearing branches. Note the dark cell contents of the epidermal cells and the subtriangular spore in the sporangium. Surange Coll., No. B.70. × 100.

FIG. 7. Tangential longitudinal section of a small branch giving off a still smaller branch. Note the dark epidermal cell contents. Surange Coll., No. B.33. × 80.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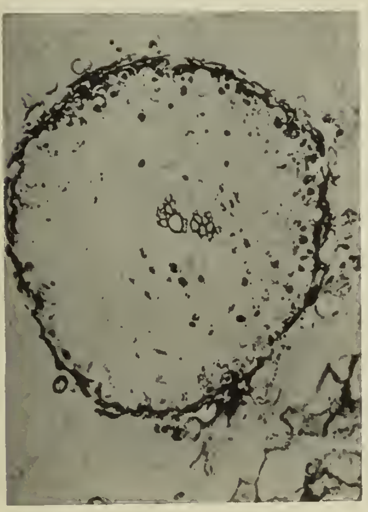
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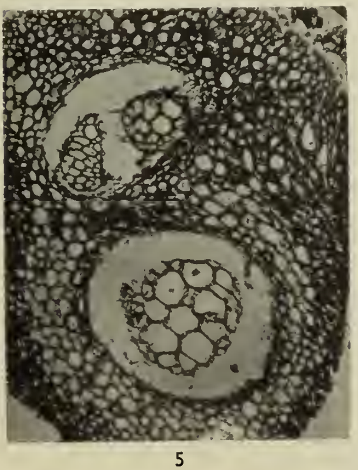
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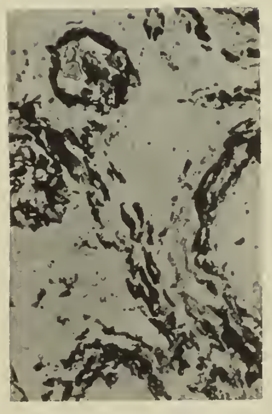
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BOTRYOPTERIS